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L. O. HOWARD, Entomologist and Chief of Bureau.

MISCELLANEOUS PAPERS.

A RECORD OF RESULTS FROM REARINGS AND DISSECTIONS OF TACHINIDÆ.

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INTRODUCTION.

It seems opportune to present, for the benefit of those interested, a preliminary announcement of some of the results secured in the course of the work connected with the rearing of Tachinidæ, carried on under the direction of Dr. L. O. Howard, Chief of the Bureau of Entomology, at the Gipsy Moth Laboratory, Melrose Highlands, Mass. Credit is due to assistants for carrying out the details of much of the work, as well as for some originality on certain points. Mr. W. R. Thompson has made all the dissections and prepared all the early-stage material for permanent preservation, both microscope slides and alcoholics, all of which work has been performed most admirably. He perfected the method of bleaching the puparia so as to show the anal stigmata to the best advantage in a slide mount. He has also done all the photographic work. Mr. D. H. Clemons has been continuously employed on the investigation of the reproductive habits of the various species in the outdoor cages, in which work he has shown much ability. He made the startling discovery of the leaf-larviposition habit of *Eupeleteria magnicornis*. Mr. T. L. Patterson has attended continuously to the Japanese Tachinas, and secured from them the maximum day's record of oviposition.

As this work was entirely new, practically nothing having ever before been attempted in the way of systematically rearing tachinids from egg to fly, it called for considerable ingenuity and much originality of method. It further developed, almost at the outset, that the various species were by no means uniform in their habits of reproduction; in fact, so greatly did they differ in this respect that a method adapted to one was by no means sure to succeed with another. The first two species studied furnish an apt illustration of this point. They were *Parexorista cheloniæ* Rond. and *Blepharipa scutellata* R.–D. The former is practically confined to *Euproctis chrysorrhœa* L. and the latter to *Porthetria dispar* L. Both are single brooded.

It was found necessary, in order to secure proper mating and oviposition in confinement, to devise a cage that would approximate natural conditions. Such an one was constructed out of doors, and consisted of just enough wooden framework to support a wire-screen inclosure 7 feet in three dimensions with a canvas top for protection

FIG. 25.—Outdoor cage for rearing Tachinidæ, with vestibule. (Original.)

against sun and rain. Into this cage (see figs. 25 and 26) were put several hundred flies of the above two species. The "tanglefooted" trays devised by Mr. W. F. Fiske, containing young caterpillars of *Euproctis chrysorrhœa* and *Porthetria dispar*, were strung on wires within. The caterpillars can not get out of these trays, which

are open above, and the flies have free access to them. The invention of this tray is what made success possible with this cage. Food was provided for the flies in the shape of bananas and other fruit cut and sprinkled with sugar, and wet sponges supplied them with requisite moisture. This cage, thus furnished, proved to be a perfect success, although some supplementary devices were found necessary for certain species as the work progressed. The flies mated freely therein and were apparently as much at home as in the open.

FIG. 26.—Outdoor cage for rearing Tachinidæ, showing disposition of "tanglefooted" trays within the cage. (Original.)

PAREXORISTA CHELONIÆ Rondani.

No difficulty was encountered in securing oviposition on the part of *Parexorista cheloniæ*, which deposited its elongate, cylindrical, whitish, thin-shelled, and pediceled eggs freely on the small caterpillars of *Euproctis chrysorrhœa* just out of the nests. The maggots, upon the hatching of the eggs, penetrated the caterpillars and a good

number of them were reared to the puparium in the trays. The four stages of the maggot were secured by opening some of the caterpillars from time to time. Thus the entire life-history was worked out for the species, so that now the egg, any stage of the maggot, and the puparium as well as the fly can be identified. The entrance of the newly hatched *chelonia* maggot into the young *chrysorrhœa* caterpillar was observed through a binocular microscope.

It must be stated here that, as a preliminary to the rearing work, the puparia of the various species were carefully studied, and it was found possible to identify them by the characters of the anal stigmata, which are very constant in the same form and furnish a variety of design in the various species that was totally unlooked for. By this means the puparia were sorted into species before the issuance of the flies.

The last stage of the maggot of *Parexorista chelonia* can always be told by the similarity of its anal stigmata to those of the puparium. The first stage, newly hatched from the egg, is very similar in the various forms of the true tachinids in having the body segments furnished with rows of minute, posteriorly directed spines, which aid the maggot in progression over the skin of the caterpillar and in entrance through the same. Its anal stigmata are not the same as those of the last-stage maggot. The second stage is characterized by the absence of a large proportion of the spines, especially those of the middle segments, and its anal stigmata begin to look like those of the last stage. The penultimate stage is the most interesting of all, and develops an unusual feature, hitherto not understood. The maggot of the first two stages derives no air from the outside, but in the penultimate stage it protrudes the pointed anal end through the skin of the caterpillar. This anal end of the penultimate-stage maggot is highly chitinized by virtue of its exposure to the air, and terminates in a pointed tube, which is curved in some species, and within the base of which lie the anal stigmata. Through this extruded tube the maggot procures air. Certain observers had already noted that some tachinid maggots protrude the anal end through the skin of the host, but it was supposed that certain species had this habit in all stages of the maggot, while others had not, since maggots are often found free inside the host.

The truth, however, is that the penultimate stage of many tachinid maggots, and this stage only, possesses this peculiarity. The last-stage maggots of these species live free inside the hosts, their cast, penultimate-stage, chitinized anal skins remaining *in situ* in the skin of the caterpillar at the point where they passed that stage. We have repeatedly dissected these anal skins from caterpillars containing last-stage maggots. The description of the maggot stages given above applies well to *Parexorista chelonia*. A few species, which will be

noted later on, not only remain as last-stage maggots within the chitinized anal skin of the preceding stage, but even transform to puparia therein, inside the caterpillar skin.

BLEPHARIPA SCUTELLATA Robineau-Desvoidy.

It was naturally inferred at this stage of the work that the reproduction of *Blepharipa scutellata* would be found as simple as that of *Parexorista cheloniæ*. Such inference was wide of the mark. All efforts to observe oviposition on the part of *scutellata* or to secure the deposited egg proved futile. The flies mated freely, remaining in copula four or five hours in some cases, but the females, unlike those of *cheloniæ*, paid no attention to the caterpillars. They even manifested alarm when the caterpillars were placed near them. In several instances they were observed to touch the ovipositor feebly to the surface or edge of the leaves upon which the caterpillars in the trays had been feeding. The supply of *scutellata* flies was limited, and it was not until this supply was exhausted that the truth dawned upon us. By dissecting dead females we secured the eggs, which were found to be minute and black, with a thin chitinized chorion, and about one-fortieth or one-fiftieth the size of those of *Parasetigena segregata* Rond., although the fly is ordinarily considerably larger than that species. The whole experiment recalled the observations of Sasaki[a] made twenty-two years ago on the Uji parasite (*Crossocosmia sericariæ* Corn.) of the silkworm in Japan. Sasaki's statements had been received with considerable incredulity by European students, but no longer seemed so improbable to us in the light of our investigation of *scutellata*, which, by the way, is extremely closely related to the Uji parasite. Every circumstance in connection with the strange behavior of the females of *scutellata* pointed directly to a habit of leaf-oviposition, the eggs to be swallowed by the caterpillars and hatched within their alimentary canal. When this conclusion had been definitely reached, no eggs of *scutellata* were on hand for experimental purposes. The conclusion had come very slowly, and was at first only doubtfully and reluctantly accepted.

PALES PAVIDA Meigen.

Soon after this, however, a similar case was encountered in *Pales pavida* Meig., a summer-issuing, two-brooded species, the flies of which began to emerge from the early-summer importations of puparia from Europe. The females of *pavida* acted in exactly the same way as did the females of *Blepharipa scutellata*. No deposited eggs could be secured, but the females were opened as they died and the eggs found

[a] Sasaki, C.—On the Life History of *Ugimya sericaria* Rondani. Journ. Coll. Sci. Imp. Univ. Japan, Vol. I, pp. 1–39, Pls. I–VI. Tokyo, 1887.

to be practically the same as those of *scutellata*. Some of these eggs, taken from a dead and dried female, were placed on pieces of leaf and fed to several species of caterpillars. The excrement of these caterpillars was carefully examined the next day and many of the eggs found therein, most of them empty, but two from the excrement of an arctian had passed through entire. The bits of leaf that this arctian (*Diacrisia virginica* Fab.) had swallowed with the eggs were in many cases six to eight times as large as the egg, conclusively demonstrating that these minute tachinid eggs can be swallowed entire by caterpillars with their food without injury to the egg. The arctian was opened nine days after, and a small *pavida* maggot, probably in its second stage, was found in the midst of a fat body next the alimentary canal. Thus the first step was gained toward a verification of the existence of this remarkable and hitherto reluctantly credited leaf-ovipositing habit in certain tachinids, including the removal from Sasaki of the stigma under which his startling observations had placed him.

ZENILLIA LIBATRIX Panzer.

A second step, which, in our opinion, practically removes all lingering doubt of the truth of our conclusions, was taken when *Zenillia libatrix* Panz. was studied. This is another summer-issuing, double-brooded species, whose eggs are quite similar in all characters to those of *Pales pavida* and *Blepharipa scutellata*. Although our supply of the flies was extremely limited, yet the very few females under observation, while they did not reach the point of actual oviposition, lived long enough to give us a decided insight into their habits.

We have found that female tachinids, when nearing their ovipositing period, will attempt oviposition and simulate with the ovipositor the action of an ovipositing female. In many instances we have observed ovipositing females make repeated attempts, thrusting the ovipositor at the caterpillars several times before actually depositing an egg. The last two of the *libatrix* females—which, by the way, had manifested the same alarm at the proximity of caterpillars as had the females of *P. pavida* and *B. scutellata*—were seen to touch the ovipositor excitedly as many as thirteen successive times to the newly eaten edge of a leaf where caterpillars had just been feeding. No egg was deposited, but the action showed the intent and, in our opinion, conclusively indicates the habit. About 150 mature eggs of *Z. libatrix* were secured from the last two females, after these died, and were fed on pieces of leaf to caterpillars of *Euvanessa antiopa* L., *Melalopha inclusa* Hbn., and *Schizura concinna* S. & A. The result of this experiment remains to be seen, but I hazard the prediction that *Z. libatrix*, *P. pavida*, and *B. scutellata* will all be found to possess the leaf-ovipositing habit.

Two other European species—as yet undetermined, but which I refer doubtfully to *Masicera* and *Phorocera*—both reared from *Euproctis chrysorrhœa*, have similar eggs and doubtless have the same habit.

PROBABILITY OF AN EXTRA MAGGOT STAGE IN LEAF-OVIPOSITING SPECIES.

It should be mentioned here that in all probability *Blepharipa scutellata*, *Pales pavida*, *Zenillia libatrix*, and the other flies belonging to this group have an additional maggot stage over other tachinids, since the newly hatched maggot is so very much smaller in size than are those of the latter. It ranges from one-tenth to one-fiftieth the size of the newly hatched maggots of those species which deposit eggs or maggots on the caterpillars, or maggots on the leaves, and yet is often much larger in the last stage than are they. In such case its second stage would correspond to the first stage of the other tachinid maggots, and would not show the last-stage type of anal stigmata. This is the case with the maggot of *P. pavida* above mentioned, which is evidently in its second stage and whose anal stigmata do not yet show the four slits of the last-stage maggot. Each anal stigma appears as a bifid plate with scalloped edge, indicating a further split of each half at the next molt, which would produce the last-stage type.

THE DEPOSITION OF LIVING MAGGOTS BY TACHINID FLIES.

We come now to another phase of tachinid reproduction. It has long been known that *Sarcophaga* and its immediate allies deposit living maggots. It was not definitely or generally understood, however, that many true tachinids do the same thing. A remark made by Lowne in his Anatomy of the Blowfly, to the effect that both *Sarcophaga* and *Tachina* (these names evidently used in the wide sense) deposit living maggots, and the records cited by Brauer in Die Zweiflügler des kaiserlichen Museums zu Wien, Volume III, that *Echinomyia grossa*, *Miltogramma conica*, and *Trixa* are larviparous, are the only references I have seen to this fact. We found before we had gone very far, however—in fact, this point developed with *Parexorista chelonia*—that female tachinids of certain species may deposit eggs practically undeveloped, or at any stage of the development of the embryo, or perhaps may even deposit living maggots.

It should be stated here that the eggs of muscoidean flies originate in tubes called the egg-tubes, a cluster of which forms an ovary. The egg-tubes of each ovary open through a single tube into the oviduct. The eggs, upon reaching full size, pass from the egg-tubes of an ovary through the single tube into the oviduct, at the lower end of which they are fertilized by the male element proceeding from the minute

long tubules which lead to the three spermathecæ or seminal vesicles. The latter receive the male fluid at the time of union of the sexes. The point of opening of the spermatic tubules marks the termination of the oviduct, immediately below which begins the long, tube-like, coiled uterus.

Upon dissecting dead females of *Parexorista cheloniæ* the uterus of certain of them was found to be packed not only with eggs but also with living maggots. The latter occurred at the lower end of the uterus next the ovipositor. As many as three hundred such eggs and maggots were found in the uterus of one *cheloniæ*. This explained why no definite period of time could be ascertained for the hatching of the egg of *cheloniæ* after its date of deposition. Some of the eggs hatched almost immediately after being laid upon the caterpillars, while others did not hatch for a week. After making this observation we realized that some of our species might be expected to deposit living maggots.

DEXODES NIGRIPES Fallen and COMPSILURA CONCINNATA Meigen.

The expectation that some species of Tachinidæ would deposit living maggots was immediately realized in the next species taken up, *Dexodes nigripes* Fall., a common summer-issuing species reared from both *Euproctis chrysorrhœa* and *Porthetria dispar*. The uteri of the females of *nigripes* were commonly found to contain living maggots, and these were apparently deposited, not on, but inside the skin of caterpillars of both *E. chrysorrhœa* and *Hemerocampa leucostigma* S. & A., and reared to the puparium in both. A very similar species, *Compsilura concinnata* Meig., apparently has the same habit of depositing living whitish maggots inside the skin of the caterpillars, and was reared in small caterpillars of *chrysorrhœa* from cold storage, not only to the puparium, but to the fly as well, thus proving at least three broods in one season for this species. It should also be stated that the above puparia of *Dexodes nigripes* similarly gave issuance to the flies, thus proving that it also has at least three broods.

The very remarkable point brought out in the investigation of these two species is that the females of both are provided with a long curved sheath, into the base of which the ovipositor fits, and which tapers to a microscopically sharp point. With this organ the females evidently puncture the skin of the caterpillars at the moment of larviposition, introducing the living maggot within the skin of the host. Such a habit was never suspected in the Tachinidæ. We have examined native species which are furnished with the same sheath and must have the same habit.

EUPELETERIA MAGNICORNIS Zetterstedt.

One of the next species taken up was *Eupeleteria magnicornis* Zett., which proved to be most remarkable as regards startling deviations from the previously known manner of reproduction among tachinids. The females of this species were most carefully labored with for a week or more in the attempt to secure their oviposition, using all kinds of caterpillars available. All efforts were in vain. Some dead females had been dissected and found to contain elongate, whitish, slightly curved eggs. It was not realized at the time that these females were immature so far as the development of the eggs in the uterus was concerned, and thus it was inferred that the species would deposit large elongate eggs on the caterpillars. It seemed quite inexplicable, therefore, when the females proved to be as much alarmed at the close proximity of caterpillars as were the females of *Blepharipa scutellata*, *Pales pavida*, and *Zenillia libatrix*. From the nature of the eggs it was impossible that they could be deposited on the leaves and eaten by the caterpillars. But why, then, should the females be so alarmed when brought face to face with the caterpillars? After much patient observation and experiment this question was answered. The flies were found to deposit living maggots, not on or in the caterpillars, but, most remarkable to relate, on the green shoots, leaf-stems, leaf-ribs, and even sometimes on the surface of the leaves!

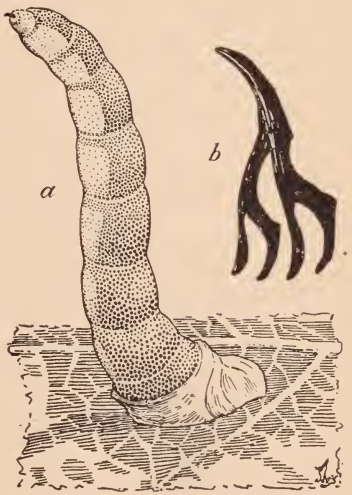

FIG. 27.—*Eupeleteria magnicornis*: *a*, First-stage maggot attached to leaf, awaiting approach of a caterpillar; *b*, enlarged mouth-hook of maggot. *a*, Greatly enlarged; *b*, highly magnified. (Original.)

The females would hover in the air about the shoots after the manner of syrphid flies, looking for caterpillars. They gave preference to the stems in depositing their maggots, and usually placed them where a silken thread had been left by a caterpillar as it climbed along a stem or over a leaf. Perhaps the sense of smell guided them in their larviposition on these silken threads. Several species of caterpillars were used with equal success, and it was found that the females would not deposit their maggots on shoots where caterpillars were not present. In fact it seemed necessary that caterpillars should have first crawled over the stems and leaves. The maggots are securely attached to the surface of the leaf or stem at the moment of deposition, by a thin membranous case, which is cup-shaped

and surrounds the anal end of the body. Attached to the leaf or stem by this base, the maggot (see fig. 27) is able to reach out in all directions as far as its length will permit—and it is much more slender and elongate than those maggots which hatch from deposited eggs. It is constantly in motion when it feels the proximity of a host. As the maggot is deposited on the silken thread with which a webworm or caterpillar of *Euproctis chrysorrhœa* marks its trail as it leaves the nest, the caterpillar is sure to pick it up in following its thread back. Doubtless the flies larviposit only on freshly laid strands, which have not lost the odor of the caterpillar. When the maggot is left undisturbed for a time it appresses its body longitudinally to the surface of the stem or leaf-rib to which it is attached. But the moment it is touched by any object it immediately becomes extremely active, striving to attach itself to the looked-for host. As soon as it lays hold on a caterpillar the motion of the latter and the exertions of the maggot itself pull it loose from the membranous cup-shaped base, which remains where it was attached.

It is probable that this habit of larviposition in *Eupeleteria magnicornis* has been developed on account of the advantage gained thereby in the certainty of attachment of the maggot to a caterpillar. Being deposited where the caterpillar must pass over it, the maggot can attach itself with great ease to the legs or underside of the caterpillar, where the hairs are few and short. It would be much less certain of attachment if the female attempted to deposit it directly on the caterpillar. The fly is large and would unduly alarm the caterpillar, which would make frantic efforts to shake the maggot off. In this it would often succeed before the maggot could find its way through the barbed hairs that protect the upper and lateral surfaces of the caterpillar's body.

The maggot of *Eupeleteria magnicornis*, as might be expected, in view of its deviation in habit from the maggots of those species previously studied, has the integument quite different in character, since it must remain for a considerable time outside the host. The species which deposit living maggots on the caterpillars, as well as those which deposit eggs, have a whitish, thin-skinned maggot. The maggot of *magnicornis*, however, has a tougher skin and is quite dark in color. In the opinion of the writer, it is one of the most specialized tachinid maggots known, although the body shows 13 very distinct segments. The integument, both dorsal and ventral, is furnished with minute, slightly chitinized, scale-like plates, save only the median ventral region. Those of the dorsal region are distinctly larger and more chitinized than are those of the lateral ventral region, but the median ventral surface of each one of the body segments except the anal is entirely without them, being furnished instead with a band of minute black spines, which are entirely lacking on the dorsal surface. Thus

it is readily seen that this maggot is especially well adapted both to remain a very considerable time in the air and to cling to and make its way over the skin of the caterpillar as soon as the latter presents itself.

This species possesses the further peculiarity of transforming to its last maggot stage inside the chitinized anal penultimate-stage skin, and also of changing to the pupa within the same, the whole remaining inclosed in the caterpillar skin. As a consequence the puparium is very thin and light colored, since it is protected from the action of both light and air by the caterpillar skin as well as by the penultimate-stage maggot skin.

ZYGOBOTHRIA NIDICOLA Townsend.

Zygobothria nidicola Towns. is another species which has exactly the same habit of last-stage maggot and puparium as that just described for *E. magnicornis*. It is an extremely interesting species in many ways. The two sexes are so different in appearance that they might be taken for distinct species or even genera. The males, in our experiments, began issuing from the puparia much in advance of the females. The species has been reared from *Euproctis chrysorrhœa* only, and then under such conditions as to indicate that the females oviposit on the young caterpillars in the fall, the young maggots hibernating in the *chrysorrhœa* nests with the young caterpillars. For this reason it was named *nidicola*. Though the sexes are so different, the fact that they belong together has been proved by their issuance from puparia having the same anal stigmata. No oviposition was secured, but by dissecting females the ovarian eggs were found to be elongate, whitish, and much like the unhatched uterine eggs of *Eupeleteria magnicornis*.

ZYGOBOTHRIA GILVA Hartig and CARCELIA GNAVA Meigen.

Zygobothria gilva Hartig is a close relative of the preceding species, but has been reared by us from *Porthetria dispar* only. Its egg, which has been found by dissecting the female, is quite similar to that of *Zygobothria nidicola*.

Of somewhat the same character is the egg of *Carcelia gnava* Meig., which has been reared from both *Euproctis chrysorrhœa* and *Porthetria dispar*. The deposited egg of *gnava* has been secured. The fly places its eggs on the caterpillar. The egg is not as slender as that of *gilva*.

PARASETIGENA SEGREGATA Rondani.

The last group of species with which we have to deal is characterized by depositing, on the caterpillars, eggs more or less oval in shape, of comparatively large size, with one exception whitish in color,

and having a moderately or quite thick chorion. The first of these species that we took up was *Parasetigena segregata* Rond., which issued from hibernating puparia along with *Blepharipa scutellata*. For a time it was confused with the latter species, since only a dozen or so specimens issued and these were not at first examined with a lens. The radical difference in the behavior of the females soon attracted our attention to their distinctness from *scutellata*. The females were not alarmed at the close proximity of large caterpillars of *Porthetria dispar*, but, on the contrary, were highly excited to oviposition by them, repeatedly and most enthusiastically and energetically ovipositing upon them whenever the caterpillars were placed near. This is apparently a single-brooded species.

TACHINA AND ALLIES.

Tricholyga grandis Zetterstedt, *Tachina larvarum* Linnæus, and *Tachina utilis* Townsend are closely related to each other and all deposit very similar eggs, which are much like those of *Parasetigena segregata*, but somewhat narrower and more elongate in shape and with a thinner chorion. They are all deposited very freely upon caterpillars. The species of *Tachina* are at least double-brooded, and the second generation of *T. grandis* has been recently reared by us to the fly, showing it to be three-brooded.

The egg of an undetermined European species, which I refer doubtfully to *Hemimasicera*, is similar to these in all characters except that it is of a decidedly light-yellow color. The eggs of this group of species are normally deposited in a practically undeveloped stage of the embryo.

Two Japanese species of *Tachina*, representing in Japan the European *T. larvarum* and *T. utilis*, but specifically distinct from them, have the same character of eggs and belong in the group with *Parasetigena segregata*, just mentioned. What has been said of this group applies to them.

TACHINA CLISIOCAMPÆ Townsend.

An American species of *Tachina*, which I identify as *clisiocampæ*, also deposits the same kind of eggs. It has been reared from both *Euproctis chrysorrhœa* and *Porthetria dispar*. An interesting point has recently been determined in connection with it. It oviposits very freely on large caterpillars of *dispar* over the greater part of the *dispar*-infested area from Rhode Island to Maine. Last season great numbers of its eggs were found on the *dispar* caterpillars, a great many of which were brought into the laboratory for rearing. Not a single tachinid puparium was secured from them. The fact that no puparia could be reared from caterpillars covered with eggs seemed inexplicable. The explanation was found this season, when many

more such caterpillars were collected for rearing. In repeated instances the newly hatched maggot was observed as it escaped from the eggshell, and in none of the observed cases was the young maggot able to penetrate the tough skin of these large *dispar* caterpillars; the maggots were watched repeatedly through a binocular in their vain efforts to do so. This species, being a native, has not yet adapted itself to *dispar*. It has been reared from it to a considerable extent, but it is quite certain that in most of the cases the egg was deposited upon the smaller and younger caterpillars, whose skins are not so tough as are those of the large ones. A very few puparia were secured this season from many thousands of *dispar* caterpillars collected, showing that hardly any of the deposited eggs of the species took hold, for these eggs were common and numerously deposited. When the species does become adapted to *dispar* as a host, which it undoubtedly will eventually, it will prove a most efficient help in checking the increase of the latter.

It is very interesting to note that the Japanese Tachinas greatly resemble *clisiocampæ*, the American form. Both differ from the European *larvarum* in having a very decided, general golden tinge to the body bloom, especially that of the head and thorax. This bloom is quite distinctly silvery in *larvarum*.

JAPANESE REPRESENTATIVES OF EUROPEAN SPECIES.

Several representatives in Japan of European species have been recognized in the puparia secured from Japanese specimens of *Porthetria dispar*, a considerable quantity of such puparia having been imported from Japan the present season. The Japanese Tachinas have been mentioned above. *Crossocosmia* sp. has been plentifully received from Japan, where it represents the European *Blepharipa scutellata* and has the same leaf-oviposition habit. The fly has been reared of a Japanese *Pales* near *pavida*, which greatly resembles the European form and has the same habit. A Japanese species corresponding to that doubtfully referred (p. 106) to *Hemimasicera* has issued from the puparium, and differs from the European form in its darker coloring and golden instead of silvery bloom. Species representing *Compsilura concinnata*, *Zygobothria gilva*, and *Carcelia gnava* have also been found in the Japanese puparia.

IMPORTANCE OF STUDYING THE UTERINE EGGS OF TACHINIDÆ.

It has developed during the progress of the work that a study of the uterine eggs of tachinids is of primary importance in the investigation of the various species. Certain very positive deductions may be drawn from them as to habit of reproduction. Before securing

oviposition—and it has been seen that one is often baffled for a considerable time in effecting this—the females can be opened and the uterine eggs obtained. Those eggs contained in the upper extent of the uterus are of course the most recently fertilized and the least developed of the uterine eggs. If they have a very thin shell it is probable that they hatch within the uterus, and that the female therefore deposits living maggots. Such is the case with *Dexodes nigripes*, *Compsilura concinnata*, and *Eupelcteria magnicornis*, and with such dexiine and macronychiid flies as we have studied: and from the character of the eggs such is possibly the case with *Zygobothria gilva* and *Z. nidicola*, though only ovarian eggs of the last have as yet been secured. Furthermore, if the hatched uterine maggot is furnished with a membranous encasement of its anal end, it shows that this maggot is not to be deposited on the caterpillars, but is to be attached to the stems or leaves. Such is the case with *magnicornis*. The uterine maggots of *nigripes* and *concinnata* have no such anal membrane of attachment, and are introduced into the caterpillars. If the uterine eggs are slender and very elongate it is quite certain that they hatch in the uterus. Such is the case with the dexiine and macronychiid flies.

If, however, a thin-shelled egg is furnished with a pedicel, this is proof positive that the egg is intended to be deposited as such, but the thin shell indicates that it is normally deposited at an advanced stage of development of the embryo. Such is the case with *Parexorista chelonia*, whose eggs have a pedicel, and should normally hatch soon after deposition. The few occurrences of hatched maggots in the uterus of *chelonia* were doubtless due to an abnormal hatching of the eggs after the death of the females. No doubt, however, *chelonia* is in process of transition from an ovipositing to a larvipositing habit. It is greatly to the advantage of the species that the egg should hatch shortly after deposition, for this guards against its loss by molting. We have found that a large percentage of the eggs are molted off by the caterpillars. Those species which deposit living maggots derive a still greater advantage in this direction. Those eggs which have a thick shell are intended to withstand atmospheric conditions for some time, and may be deposited a week or more before the embryo is fully developed. Such is the case with *Parasetigena segregata*, *Hemimasicera* sp. (?), *Tricholyga grandis*, *Tachina larvarum*, *T. utilis*, *T. clisiocampæ*, and the Japanese Tachinas. That the eggs of these are large shows that they are to be deposited on the caterpillars.

Again, if the eggs are minute it is quite certain that when matured they will be black and highly chitinized, and each character points directly to a habit of leaf-oviposition. The chitinization indicates that the eggs are intended to withstand exposure to the elements and

to be swallowed. Equally indicative is minuteness, for otherwise the eggs could not be swallowed entire. It is probable that such eggs, deposited on leaves and intended to be swallowed, remain unchanged without losing their vitality for a very considerable period of time, until they are swallowed by the caterpillars. It is equally probable that such eggs are not deposited until the embryo is nearly or quite fully developed, and that the digestive juices and conditions which the egg encounters in the alimentary canal of the caterpillar act upon the chitin and cause the shell to weaken so as to release the maggot. It is certain that such eggs must hatch within a very few hours after being swallowed, otherwise they will pass out with the excrement. One of the fed eggs of *Pales pavida*, above noted, passed through a *dispar* caterpillar in about four hours. A minute egg can not have a thick chorion and is therefore provided with a chitinized thin one, which withstands atmospheric conditions equally as well as, or better than an unchitinized thick one. Furthermore, the chitinization strengthens the egg and thus lessens the chance of injury to it while being swallowed. Still further, we have found that the chorion of all these eggs possesses a minute raised reticulation, which we consider is intended as a framework to strengthen it so as to protect the egg still more fully from injury in being swallowed. Such are the eggs of the *Blepharipa scutellata* group above described, which includes *Pales pavida* and *Zenillia libatrix*. The chorion reticulation of *cheloniæ* and other tachinid eggs is not so thickened and raised.

Enough has been said to show how very largely the reproductive history of the species may be read from the uterine eggs, which can be dissected from almost any female fly, collected or otherwise. It is only necessary that the female be fertilized. Even the ovarian eggs from unfertilized females show a great deal, for we have noted that the ovarian eggs of *Parexorista cheloniæ* show the pedicel while still enclosed within the egg-tubes.

REPRODUCTIVE CAPACITY OF TACHINIDÆ.

The capacity for reproduction in the females of the various species of Tachinidæ is another very interesting subject, of which surprisingly little is known. The greatest number of eggs that we have noted in the uterus of *Parexorista cheloniæ* is about 300, but this number may not represent the full capacity of the females for reproduction. After the uterus is well filled, further eggs may reach it from the ovaries until its extreme limit of distension is finally attained, and still more may follow as the contents are deposited. The uterus of a female of *Eupeleteria magnicornis* which had begun larviposition was found to contain, at a conservative estimate made from actual count of a portion, 3,200 eggs and maggots. This did not represent the full capacity of the female, for the egg-tubes in the

ovaries still contained ova. The uterus in this specimen was very long and coiled, and greatly distended by its contents. This is a high record of reproductive capacity. It is quite probable, however, that *Blepharipa scutellata* exceeds even this record, for the fly is large and the egg minute. Besides, a habit of leaf-oviposition would presuppose a lavish productiveness of eggs. Sasaki estimates a capacity of over 5,000 for *Crossocosmia sericariæ*, and some of our native species having the same habit equal this estimate. *Tachina* and its close allies deposit a great many of their comparatively large eggs, but their capacity does not seem to much exceed 100, judging from those we have opened. The other species that we have so far studied have, upon dissection, shown from 100 to 5,000 uterine eggs. The uterus of a native macronychiid fly, *Microphthalma trifasciata* Say, which deposits living maggots, was found by us to contain some 2,000 eggs and maggots. Native species having the leaf-larviposition habit commonly show from 2,000 to 3,000 uterine eggs and maggots, and those having the leaf-oviposition habit run up to 5,000 uterine eggs. The genera of these are given farther on.

THE REARING OF TACHINIDÆ IN CONFINEMENT.

It had currently been supposed that the oviposition of tachinids in confinement was a most difficult thing to secure. With proper facilities at hand, such is by no means the case. The Riley rearing cage, large or small, is not at all adapted to the work, yet some species may be induced to oviposit in it, and even in the very restricted space under a jelly glass. The proper cage for this work is our large out-of-doors wire-screen cage, which is shown in figures 25 and 26. For indoor rearing of single caterpillars bearing eggs or containing maggots we have adopted the glass cylinders shown in figure 29. These have the top covered with cheesecloth, and are placed on a stand which consists of a simple cloth-covered frame 5 inches square. Two opposite sides of the frame are made higher than the other two, for the completed stand to rest on, so as to allow circulation of air beneath. Cheesecloth will not do for the covering of the frame, since the mesh will permit tachinid eggs and small maggots, or even small caterpillars, to escape. For the same reason cheesecloth will not do for the bottom of the "tanglefooted" trays. We have known full-grown maggots to work through it with ease. For both frames and trays a more closely-woven cloth should be used. Flies also can be placed in the glass cylinders, but a little dry sugar and a bit of wet sponge should be included with them. Many species will live for two or three weeks in this way. These cylinders are especially adapted to rearing tachinid maggots in single caterpillars, either indoors, or, during warm weather, in one of the large cages outdoors, which may advantageously be furnished with shelves for this purpose.

In our large outdoor cages we have been greatly struck with the extreme docility of the ovipositing female tachinids. They can be handled and caused to oviposit quite at the will of the operator in most cases.

AN IMPROVEMENT IN THE METHOD OF COLONIZING TACHINIDÆ.

The extreme ease with which oviposition was secured in the cases of *Tricholyga grandis* and the Japanese and European Tachinas in the outdoor cages suggested the feasibility of an improvement in the method of colonization hitherto practiced. Until this season only the flies themselves had been liberated, but recently the plan has been adopted of colonizing caterpillars upon which the tachinids have been induced to oviposit, in conjunction with the liberation of the flies. Egg colonization, or the colonization of the caterpillars with the eggs on them, is a step in advance of fly colonization, and thus gives greater assurance of success in the establishment of the species. It has proved very easy of accomplishment. Over 1,000 webworms were colonized in July with eggs of the Japanese Tachinas on them. Oviposition was secured in an outdoor cage by one assistant at the rate of 200 to 300 eggs per day during favorable weather, these being furnished by but little over a dozen ovipositing females. These flies were afterwards liberated. The cage used is shown in figure 28.

Early in August a new lot of Japanese Tachinas had become ready for oviposition in this cage, and one assistant in one day, working six hours, secured 335 eggs from them on young caterpillars of *Euproctis chrysorrhœa* from cold storage, one egg on a caterpillar. This lot of eggs came from not over 20 ovipositing females. This is a very high record of oviposition—almost an egg a minute—for it must be remembered that the caterpillars had to be exposed, one at a time, to the flies. These eggs, with others secured on other days, were colonized by placing the caterpillars on new oak growth near the laboratory, where defoliation by *Porthetria dispar* had occurred early in the season. This second lot of Japanese flies was afterwards liberated, over a thousand eggs having been secured from them on young *chrysorrhœa*, and colonized. Some of the advantages of egg colonization before liberation of the flies are the provision in the outdoor cages of food and caterpillars for oviposition, and protection from enemies preceding and during a part of the ovipositing period. Furthermore, after fly colonization, if we find eggs of the flies in question on caterpillars in the vicinity, we naturally consider the establishment of the species to be more or less assured. If, however, we colonize the caterpillars themselves with the eggs of the flies already on them, we have this assurance at the moment of colonization, which must be considered a very great advantage.

NEW ALTERNATE HOSTS FOR INTRODUCED TACHINID FLIES.

An important problem in the process of establishment of imported summer-issuing species of tachinids is that new alternate hosts must be found for them in this country. The caterpillars of *Porthetria dispar* and of *Euproctis chrysorrhœa* have mostly pupated by midsummer, both here and abroad, and are thus not available as hosts after that time. Therefore the late summer generations of these tachinids develop in certain alternate hosts which occur in their native country. Those alternates are not present here, and new alternates must be provided for them from our native species. Fortunately tachinids are quite amenable to a change of host. Gratifying results have been obtained in this direction. Tussock caterpillars (*Hemerocampa leucostigma* S. & A.), have proved very acceptable to *Dexodes nigripes*, *Compsilura concinnata*, *Tricholyga grandis*, and other species, but they are not sufficiently abundant after midsummer to be of use for egg colonization on a large scale. Caterpillars of *Datana*, *Basilarchia*, *Euvanessa*, *Anisota*, *Schizura*, *Melalopha*, and others have been found acceptable to the flies in most instances, but likewise none of these is sufficiently abundant at the right time. We were at first very much at a loss for suitable alternate host caterpillars in sufficient number. It was therefore most gratifying to find that the newly hatched fall webworms (*Hyphantria cunea* Drn.) just coming on, which were abundant and easily obtained, were admirably suited to the purpose. Profuse oviposition was secured on these from the Japanese Tachinas, and also from *Tricholyga grandis*, *Tachina larvarum*, and others. The webworms, as soon as they had been oviposited on, were put back in the webs in large colonies to insure their prosperity. The females of *Eupeleteria magnicornis* industriously deposited their maggots on webworm-infested shoots, placed with the flies inside the wire-screen receptacle shown in figure 29.

To make success more certain in the egg colonization of the Japanese and European Tachinas, oviposition was also secured on young *chrysorrhœa* caterpillars that had been kept in cold storage until about the 1st of August. Had it not been for the fact that a great amount of new and tender oak foliage was available, where complete defoliation by *dispar* had occurred during the early summer, these *chrysorrhœa* caterpillars could not have been used. The old and matured leaves are not suited to the young caterpillars just out of the nests, but the latter flourish on the new oak growth.

Thus the question of alternate hosts in this country was satisfactorily answered, not only for purposes of egg colonization, but also for the needs of the liberated flies. The flies of *Tricholyga grandis* and the first lot of flies of Japanese *Tachina*, all of which had, so to speak, been trained to webworms through much oviposition on them, were colonized in separate webworm localities. Thus it was certain

not only that their wits had been sharpened for webworms but that they would find plenty of these on which to oviposit.

Similarly, the second lot of flies of Japanese *Tachina*, which had been trained to oviposition on *chrysorrhœa* entirely, was furnished at the time of liberation with a good supply of native cold-storage *chrysorrhœa* caterpillars of fair size, placed on new and tender oak growth, the *chrysorrhœa* of the vicinity being little more than hatched

FIG. 28.—Outdoor cage for securing oviposition of Japanese *Tachina*, covered about door with paper to prevent the flies from congregating at that point. (Original.)

at the time and too small to furnish it with proper host material. Some of these caterpillars were dissected about a week later and 20 per cent of them showed living maggots of *Tachina*.

IMPROVEMENTS IN THE OUTDOOR REARING CAGE.

Experience with the outdoor cage described on page 96 has suggested two improvements, which will be put into practice the coming season. It is often highly desirable to be able to admit all the sunlight and warmth available in the Massachusetts climate. For this

purpose the canvas roof should be capable of being shifted completely to one side, so as to admit the sun, and swung back over the cage again during bad weather and at night. The cage used for the Japanese *Tachina* was made without any roof, being open to the sky through the wire screening. Tarred roofing was placed over it when needed. This proved to be a very great advantage.

The second improvement will consist in a raised cement floor to extend a foot all around outside the wire screen, this outside portion to contain a shallow trench that should be kept constantly supplied with a little kerosene on water. This will obviate all difficulty from ants, carabids, and spiders, which will often kill the flies if not care-

FIG. 29.—Glass cylinders in use in rearing Tachinidæ, and wire-screen receptacle for inclosing flies with caterpillars on foliage. (Original.)

fully watched. The floor can be sloped slightly inside the cage, so as to drain off through a pipe to be carried beneath the kerosene trench. Next season there will also be erected a separate cage of this description fitted with shelving to accommodate the numerous glass cylinder stands necessary for the rearing of the different stages of tachinids separately in caterpillars, which can be accomplished much better under out-of-door conditions.

Attention should be called to the wire-screen vestibule with which our first outdoor cage was furnished (shown in fig. 25). This was found quite necessary in order to prevent the flies from escaping while the experimenter is going in and out of the door, certain species being

extremely active during warm, sunny weather. Figure 26 is introduced to show the disposition of the "tanglefooted" trays within this cage. Figure 28 shows the outdoor cage used in securing oviposition of Japanese *Tachina*, which, in default of a vestibule, was covered about the door with paper to prevent the flies from congregating there. Figure 29 shows the glass cylinders in use and the wire-screen receptacle for inclosing flies with caterpillars on foliage that can be kept green for a considerable time.

We further have in mind for next season a compound outdoor cage on these lines, 30 by 15 feet floor space, arranged with five compartments on each side of a passageway, each compartment to be 6 by 6 by 6 feet, so as to allow one experimenter to work separately with 10 species of flies at a time. The whole will be fitted with canvas roof and drop curtains, in sections, capable of being completely rolled up or lowered, as desired. A small table, with microscope and work materials for the use of the experimenter, will be placed at one end of the passageway. The other end of the latter will open outside by a screen door, and each compartment will open into the passageway only. The vestibule can thus be dispensed with, since the passageway will serve the purpose.

BLEACHING THE PUPARIA OF TACHINIDÆ.

One point connected with the preparation of early-stage tachinid material for permanent preservation deserves mention. It has already been stated that the anal stigmata of the puparia show excellent characters for the separation of the various forms. It is highly desirable to present photomicrographs of these along with the taxonomic results derived from a study of them, but no practical mounts for this purpose can be made of them in their natural condition. A series of bleaching experiments has therefore been instituted, and the puparia have been successfully bleached with chlorine water to any desired degree. The result is a slide mount from which either drawings or photographs may be made with ease.

RESULTS FROM DISSECTIONS OF NATIVE TACHINIDÆ.

I am able to include here some interesting results obtained from dissections of females of native tachinids. We have secured the uterine eggs of some seventy species, and the results are a revelation. *Bombyliomyia abrupta* Wiedemann, *Echinomyia algens* Wiedemann, 3 species of *Peleteria*, 3 species of *Archytas*, *Panzeria* sp., *Varichæta* sp., *Copecrypta* (*Trichophora*) *ruficauda* van der Wulp, and *Micropalpus* sp. show uterine maggots similar to those of *Eupeleteria magnicornis*, thus proving the abundant presence of the leaf-larviposition habit in our native fauna. The maggots of some of the forms differ in the details of the spines and plates. We now know thirteen species, therefore, that have this habit.

The great fecundity and consequent importance of *Blepharipa scutellata* and *Crossocosmia* sp. as parasites of *Porthetria dispar* is strongly suggested in a native species of *Parachæta*, whose uterus we found to contain some 5,000 minute black eggs similar to those of *scutellata*. Some of these uterine eggs, upon being slightly pressed beneath a cover glass, disclosed the fully formed maggots, which fact proves our supposition that eggs of the leaf-ovipositing species are ready to hatch at the time of deposition. Sasaki has shown this to be the case with the Uji parasite. Furthermore, the structure of the maggot itself, as well as that of the chorion, shows that the former may remain quiescent within the latter for a considerable period until the egg is swallowed by a caterpillar. The newly-hatched maggots of this group are quite as specialized as are those of the *magnicornis* group, but in a totally different direction. Those above mentioned were found to be broad-oval, considerably flattened, the anterior end slightly narrowed and pointed, and with the spines chiefly disposed on the anterior segments. There are 12 rows of spines, each segment except the last having a row, but the rows of the middle segments are very short. The first four rows, on segments 1 to 4, are complete and continuous on all sides; the next seven rows, on segments 5 to 11, are incomplete, showing from 4 to 8 spines in the middle on the ventral surface only, segments 6 to 9 having the least; the last row, on the preanal segment, is complete. The spines of the first three dorsal rows are especially strongly hooked and claw-like, the hook process of each pointing backward so as to hold the maggot in piercing the walls of the alimentary canal of the caterpillar. The spines of the other rows are also claw-like, but the hooks are less strongly developed. Last, but especially suggestive, is the fact that the lateral portions of the maggot show a row of large fat globules on each side just inside the skin, which are no doubt designed to sustain the maggot until the egg is swallowed. (See fig. 30.)

FIG. 30.—*Parachæta* sp.: Uterine egg with chorion removed, showing structure of the fully formed maggot from below. Highly magnified (original).

Gonia frontosa Say, *Pseudogermaria* sp., *Blepharipeza leucophrys* Wiedemann and a second species, *Parachæta* sp., *Latreillimyia* sp. (aberrant form from Pennsylvania), *Triachora unifasciata* Desvoidy, two species doubtfully referred to *Masicera*, *Exorista* sp., *Eusisyropa blanda* Osten Sacken, *Sisyropa* sp., and two species near *Eusisyropa* (Laboratory Nos. 1979, 2322) have all been found to have minute eggs similar in size to those of *Blepharipa scutellata*. Thus, at the very first examination of our native species we find fourteen different forms that we can say positively have the leaf-oviposition habit. Five of

the two dozen European species that we have studied are to be added to these, making a total of nineteen American and European species now known to have this habit. It is therefore evident that, while European and American students were industriously engaged in criticising and discrediting Sasaki's statements, abundant proof of them was right at hand on both continents, had anyone stopped to look for it.

The uterine eggs of the other native forms dissected indicate a habit of oviposition on, or larviposition in or on the host. The dexiine flies appear so far to deposit living maggots, slender and pointed like those of the macronychiid flies. *Theresia tandrec* Coquillett (*non* Robineau-Desvoidy) deposits the same kind of a maggot, except that its anal end is bifid into two slender processes in which the tracheæ terminate. The pseudodexiine flies deposit a maggot somewhat less elongate, and some of the masiceratine and phoroceratine flies, one still more shortened. One species near *Masicera*, but with stout discal macrochætæ, was found to contain uterine maggots that were shortened and plump, with strongly marked complete rows of spines on the segments, greatly resembling certain œstrid maggots (*Œstrus* and *Gastrophilus*). *Hemyda aurata* Desvoidy gave us only ovarian eggs, which are elongate but do not seem to indicate larviposition. So far the leaf-oviposition habit seems confined to certain masiceratine, willistoniine and goniine flies and their near relatives, which seem to form two or three compact taxonomic groups. The habit of leaf-larviposition seems confined to the echinomyiine and hystriciine flies. An immense amount of this dissecting work must yet be done, however, before any generalizations can be made.

As might be expected, there is considerable diversity of type in the structure of the chorion of the minute eggs. This may, or may not, imply independence of origin. For example, the European species doubtfully referred to *Phorocera* (p. 101) has the exposed chorion (the part not attached to the leaf surface) limpet-shaped and showing concentric rings instead of the ordinary reticulation; and the exposed chorion of *Sisyropa* sp. (Laboratory No. 1975) is reticulate, but shows a remarkable, irregular, light-colored fringe around the edge, pierced with microscopic shot-holes. Both of these forms of egg, placed on the leaves, would greatly resemble extremely small miniatures of certain coccids!

SUMMARY OF REPRODUCTIVE HABITS NOW KNOWN IN THE TACHINIDÆ.

From what has been recorded in this paper it will be seen that we now know five different styles of reproductive habit in the Tachinidæ. These may be summarized as follows:

Reproductive habits.	Examples.
(1) Host-oviposition	*Tachina larvarum.*
(2) Leaf-oviposition	*Blepharipa scutellata.*
(3) Supracutaneous host-larviposition	Dexiine flies and allies.
(4) Subcutaneous host-larviposition	*Compsilura concinnata.*
(5) Leaf-larviposition	*Eupelteria magnicornis.*

This is certainly an excellent showing for adaptation and variety of habit in a family as compact in character as the Tachinidæ, which does not include the macronychiids, muscids, or phasiids, and in which a certain unity of habit was long supposed to obtain. It may be further remarked that we have in one instance dissected two female specimens, separated with difficulty on slight external characters, and appearing at first to be the same species, and have found one to have the habit of leaf-oviposition and the other, a habit of either host-oviposition or host-larviposition. This aptly illustrates the necessity for a most careful study of external adult characters and a nice sense of discrimination—in other words, the zoological sense—in order to distinguish the many distinct but often closely similar forms of these flies. Slight differences in shade of pollinose covering, in width of front, in strength of frontal bristles, in hairiness of eyes, and in thoracic and abdominal lines—all of these easily overlooked—were the only external characters that enabled us to pronounce the two specimens distinct species. The character of the uterine eggs, however, at once demonstrated the very marked distinctness of the two forms, which can not be referred to the same genus, nor even to the same tribe, and perhaps not even to the same subfamily.

The five classes of reproductive habit mentioned above are arranged in the order of their probable antiquity, host-oviposition being considered the oldest and leaf-larviposition the most recent. This order not only seems natural from the reproductive standpoint, but is borne out by a study of the external characters of the flies themselves, principally the character of the facial plate.

CONCLUSION.

The results of all this work on European, Japanese, and American tachinids point to the very great importance of *Blepharipa scutellata* and *Crossocosmia* sp. as parasites of *Porthetria dispar*. The great capacity for reproduction, possessed by these species, and the fact that all of their eggs must be eaten by the caterpillars wherever *dispar* is abundant, place them in the lead of parasites.

No two species can be so relied upon as parasites of *Euproctis chrysorrhœa*, but the Japanese Tachinas, *Tricholyga grandis*, *Compsilura concinnata*, *Dexodes nigripes*, and *Parexorista cheloniæ* seem to be among the most important here.

All of the other imported species mentioned will prove of much importance as aids in the control of one or both of these moths. The great majority of them are parasitic on both hosts.

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